

# Occurrence and Pathogenicity of *Puccinia recondita* f. sp. *tritici* on Wheat in South Africa from 1983 Through 1985

Z. A. PRETORIUS, Senior Agricultural Researcher, Grain Crops Research Institute, Bethlehem 9700, South Africa; F. H. J. RIJKENBERG, Professor, Department of Microbiology and Plant Pathology, University of Natal, Pietermaritzburg 3200, South Africa; and ROY D. WILCOXSON, Professor, Department of Plant Pathology, University of Minnesota, St. Paul 55108

## ABSTRACT

Pretorius, Z. A., Rijkenberg, F. H. J., and Wilcoxson, R. D. 1987. Occurrence and pathogenicity of *Puccinia recondita* f. sp. *tritici* on wheat in South Africa from 1983 through 1985. *Plant Disease* 71:1133-1137.

Leaf rust (*Puccinia recondita* f. sp. *tritici*) of wheat (*Triticum aestivum*) was widespread in South Africa during 1983, 1984, and 1985 and often reached epidemic levels. Leaf rust severities were generally high on spring wheat in the Cape Province but varied on spring and winter wheat in the Orange Free State, Transvaal, and Natal. The leaf rust resistance genes *Lr1*, *Lr2a*, *Lr2b*, *Lr3a*, *Lr3bg*, *Lr3ka*, *Lr10*, *Lr11*, *Lr14a*, *Lr15*, *Lr16*, *Lr17*, *Lr20*, *Lr24*, and *Lr30* acted differentially to the isolates tested. Nine races were identified during the 3-yr period, two of which were collected only from *T. durum*. A race characterized by the avirulence/virulence formula *Lr3a,3bg,3ka,11,16,20,24,30/1,2a,15,17* was isolated most frequently (35%) in 1983. A similar race, but possessing additional virulence to *Lr24*, predominated on bread wheat in 1984 (54%) and 1985 (69%). No isolates virulent to resistance genes *Lr9*, *Lr19*, *Lr21*, and *Lr26* were found.

Leaf rust, caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* (*P. r. f. sp. tritici*), is important and widely distributed on wheat (*Triticum aestivum* L.) in South Africa. It occurs annually in most areas, but distribution and severity are influenced by climatic conditions during the growing season. Leaf rust is generally most severe on autumn-sown spring wheat in the winter rainfall regions of the Cape Province, but moist conditions and elevated temperatures during spring also promote leaf rust on winter wheat in the Orange Free State. Irrigated spring wheat throughout South Africa and durum wheat (*T. durum* Desf.) in the Fish River Valley in the northeastern Cape Province are also regularly subjected to severe leaf rust epidemics.

Many of the current commercially grown wheat cultivars in South Africa were developed primarily for agronomic characteristics and resistance to stem rust (*P. graminis* Pers. f. sp. *tritici* Eriks. & E. Henn.) with little effort toward selection for resistance to *P. r. f. sp. tritici*. Almost inevitably, all wheat cultivars officially recommended for cultivation in South Africa (2) were susceptible to leaf rust during the study period.

The value of determining genetic variation in cereal rust fungi was discussed by Roelfs (10), and race surveys

are regularly conducted in Australia (9), Canada (12), and the United States (8). These determinations provide invaluable epidemiological data for use in cooperative breeding programs by identifying isolates that have virulence that is likely to be important in a geographical area.

The physiologic specialization of *P. r. f. sp. tritici* in South Africa was last documented in 1937 by Verwoerd (15), who identified five races according to reactions of eight differential host cultivars. The lack of information regarding virulence and epidemiology of the wheat leaf rust pathogen on the sub-Saharan African continent was evident from a recent treatise on the cereal rusts (11). With the exception of a study on physiologic races of leaf rust of wheat in Kenya (6), there are no known records for other central and southern African countries.

Survey studies on the leaf rust pathogen of wheat were undertaken during 1983-1985 to determine the range and distribution of pathogen virulence in South Africa and to identify effective sources of monogenic seedling resistance. An objective of the 1983 survey was to compile a set of wheat genotypes that would differentiate virulence components of the South African population of *P. r. f. sp. tritici*. Additionally, our study provided information on survival of inoculum between growing seasons.

## MATERIALS AND METHODS

**Survey.** *P. r. f. sp. tritici*-infected wheat leaves were collected from commercial fields, cultivar evaluation trials, breeding lines, and trap nurseries. Extensively

surveyed areas were the wheat-producing areas of the western, southern, and eastern Cape Province, eastern Orange Free State, and of the irrigated areas in the eastern and central Transvaal, Natal, and northern Cape Province. Survey stops were made at commercial fields about 20 km apart and at small-grain experimental sites and trap plots along the route. Collections were also received from Transkei, Lesotho, and the durum wheat-growing areas in the Fish River Valley. In the survey results, data were grouped in agroecological geographic areas according to the origins of uredinial collections. Record was kept of the collection date of each sample and of whether isolates originated from commercial fields, trap nurseries, or breeding material. Pathogenicity of *P. r. f. sp. tritici* collected from durum wheat was evaluated separately from that of isolates established from bread wheat.

Surveys were generally conducted during October to December, when wheat crops in the different growing areas were between anthesis and maturity. In 1985, two additional surveys were conducted in the Cape Province during March and August to determine racial identity of inoculum overwintering on volunteer wheat and to monitor leaf rust incidence during the growing season. During surveys, the occurrence and distribution of some of the alternate hosts of *P. r. f. sp. tritici* (1,13) were also investigated.

The trap nurseries contained 40 entries and were planted annually at 42 locations throughout South Africa. Included in a nursery were wheat cultivars and lines universally susceptible to both leaf and stem rust as well as genotypes that carry specific genes for resistance.

**Inoculum multiplication.** Seedlings of Morocco wheat, a susceptible host, were grown in soil in 10-cm plastic pots in a greenhouse. Two days after seedlings had emerged, maleic hydrazide at 10 mg/pot was added as a soil drench to retard plant development and to enhance sporulation of the fungus (14). Urediniospores from each field collection were transferred onto 7-day-old Morocco plants, which were then placed in darkness in a dew chamber at 19 C for 19 hr; during the last 3 hr, plant surfaces were allowed to dry off gradually. Plants were then placed in a greenhouse at 18-24 C where cool-

Part of a Ph.D. thesis submitted by the first author to the University of Natal, Pietermaritzburg, South Africa.

white fluorescent tubes provided supplemental illumination of 9,000 lux for 12 hr daily.

**Differential set.** Preliminary experiments during 1983, in which 31 wheat cultivars and lines, each carrying a single (*Lr*) gene for resistance to leaf rust, were inoculated with 83 single-uredinium isolates, detected 12 *Lr* genes with clear differential ability. These genes were *Lr1*, *Lr2a*, *Lr3a*, *Lr3bg*, *Lr3ka*, *Lr11*, *Lr15*, *Lr16*, *Lr17*, *Lr20*, *Lr24*, and *Lr30*.

All of these genes, except *Lr20* and *Lr24*, are available in Thatcher wheat isolines. The genes *Lr2b*, *Lr10*, and *Lr14a*, also in Thatcher background, were added to the differential set during race classification in 1985. Seed of the Thatcher near-isogenic (RL) lines were obtained from Agriculture Canada, Winnipeg, and seed of the cultivars Thew (*Lr20*) and Agent (*Lr24*) were from the Plant Breeding Institute, Castle Hill, Australia.

**Race testing.** Differential hosts were planted in 10-cm plastic pots, and a water-soluble fertilizer (28% N) was added (20 mg/pot) when plants were 2 days old. Seedlings were 6–8 days old when inoculated, when primary leaves were fully expanded.

Each differential set was inoculated with urediniospores collected from a single uredinium on Morocco. Spores were collected in a gelatin capsule, suspended in Soltrol 130 or Soltrol 170 light weight mineral oil (Phillips Chemical Company, Borger, TX), and atomized (5) onto plants the same day spores were collected. Inoculated plants were kept in a dew chamber as described for Morocco seedlings. After completing the drying period, plants were placed in a greenhouse at 18–24 C with a 12-hr supplemental photoperiod of 9,000 lux daily.

During the three survey years, 43, 255, and 330 single-uredinium isolates from 32, 149, and 151 field collections were established, respectively, and each was

characterized on a differential set. Infection types were allocated on a scale of 0–4 (10) 10–14 days after inoculation. In our study, pathogenicity of isolates was determined according to low or high infection types mediated by *Lr* genes: infection types 0; to 2 indicated avirulence and infection types 2+3 to 4 indicated virulence in the pathogen for a resistance gene. Seedlings of Thatcher near-isogenic lines RL6010 (*Lr9*), RL6040 (*Lr19*), and RL6043 (*Lr21*) and of cultivar Kavkaz (*Lr26*) were inoculated with composite collections of urediniospores each year to identify undetected virulence characteristics. Genes *Lr9*, *Lr19*, *Lr21*, and *Lr26* had shown resistance to South African collections of *P. r. f. sp. tritici* during preliminary experiments in 1983.

## RESULTS

Spring wheat grown under winter rainfall conditions in the Cape Province was severely infected by leaf rust during the entire study period. Flag leaf severities of 100% on the cultivars SST16, SST23, SST33, and SST66 were common and restricted yields, especially in the southern Cape Province. Similar levels of severity were observed on spring cultivars grown in the irrigated areas of Transvaal and Natal, but because of the absence of winter rains in these areas, epidemics were not as widespread as in the Cape Province. In the winter wheat production areas of the Orange Free State, incidence of leaf rust was generally low and did not damage crops. Epidemic levels of *P. r. f. sp. tritici* were occasionally observed in fields of the susceptible winter cultivar Scheepers 69. During 1985, the durum wheat cultivars Fargo and Nordum were heavily infected with leaf rust, and flag leaf severities of 100% commonly occurred throughout the Fish River Valley.

The collection of 628 isolates of *P. r. f. sp. tritici* made in South Africa from 1983 through 1985 was divided into nine

pathotypes on the basis of infection types produced on wheat cultivars and lines carrying single *Lr* genes. Infection types of nine type cultures from the 1985 survey and representative of the spectrum of physiologic specialization identified in South Africa are shown in Table 1. Uredinial collections from commercial fields contributed to 54% of the 628 isolates evaluated, whereas collections from trap nurseries and breeders' plots each contributed 23% of the isolates. All pathotypes except isolate 3SA120 (Table 2) were collected from commercial bread and durum wheat fields. Apart from isolates 3SA124 and 3SA125 (Table 3), all other pathotypes identified were also collected from trap nurseries.

Infected wheat leaves were collected from various parts of South Africa each month beginning in September 1983 and continuing through December 1985. Uredinia were common on wheat leaves in the summer rainfall regions in the Orange Free State and Transvaal from January to May. During June, leaf rust occurred on early-sown wheat in the irrigated areas of the Transvaal and Transkei. From July through September, infections occurred sporadically on wheat in the Cape Province, northeastern Orange Free State, and Transvaal. Unusually wet conditions in the southern and eastern Cape Province during the summer of 1984–1985 favored development of volunteer wheat. Severe leaf rust infection was observed on plants in the eastern Cape Province, where several fields under minimum tillage ensured an abundance of volunteer plants. However, no volunteer plants were found in the western Cape Province.

*Anchusa* spp. (Boraginaceae), *Thalictrum* spp., *Clematis* spp., and other genera belonging to the Ranunculaceae have been described as alternate hosts for the wheat leaf rust fungus (1,13). A number of *Anchusa*, *Thalictrum*, and *Clematis* species occur throughout South Africa and are either indigenous or

**Table 1.** Characteristic infection types produced on wheat lines or cultivars that carry different resistance genes to nine physiologic races of *Puccinia recondita* f. sp. *tritici* identified in South Africa during 1985

Wheat line or cultivar	<i>Lr</i> gene	Infection type produced on selected lines <sup>a</sup>								
		3SA120	3SA121	3SA122	3SA123	3SA124	3SA125	3SA126	3SA127	3SA128
RL6003	1	4	4	0;	4	0;	0;	4	4	4
RL6016	2a	1c	4	;1c	4	;	2	4	4	;1=c
RL6019	2b	2	4	2=c	4	;cn	3=	4	4	2
RL6002	3a	;	;	3	;	3	3	0;	0;	3
RL6042	3bg	;	;	3	;	;	;1	;	;	x=
RL6007	3ka	;1	;1	;1	;1	3+	3	;	;	3
RL6004	10	3	2	3	2	2+3	2	3	3	4
RL6053	11	2	2	2	2	;1	;1	2	2	4
RL6013	14a	4	x	4	x	4	x	4	4	4
RL6052	15	;c	4	;	4	;	;1cn	4	4	;1=c
RL6005	16	1cn	1cn	3	1cn	2c	3=	1cn	1cn	1cn
RL6008	17	;	;1c	;1+	;1c	;	;1c	4	4	;1c
Thew	20	;	;1	;1	;1	4	4	;	;	4
Agent	24	;	;1cn	;c	4	;1	;	;	4	4
RL6049	30	2	2	2	2	3+	3	;12	;12	3+

<sup>a</sup> Infection types are according to a scale of 0–4 (10). Classes 0; to 2 and x indicate avirulence, and 2+3 to 4 indicate virulence in pathogen for a resistance gene. Plus or double minus signs denote gradations above or at lower size limit for an established infection type class, and c or n indicate the association of chlorosis or necrosis with a lesion.

introduced (M. Welman, *personal communication*). *Anchusa capensis* Thunb. is commonly found in South Africa and was described as an aecial host for leaf rust of rye in the United States (3). Large populations of *A. azurea* Mill. also occur adjacent to wheat fields in the western Cape Province. However, no aecial infections on any of these hosts have been observed or reported in South Africa despite the frequent production of teliospores on mature wheat leaves.

Although *Lr2b*, *Lr10*, and *Lr14a* were not tested as differentials during 1983 and 1984, type cultures from that period corresponded with type cultures from 1985 when tested together on the expanded set of differentials. Thus, isolates 3SA77 and 3SA120; 3SA61, 3SA57, and 3SA122; 3SA73, 3SA78, and 3SA121; 3SA62, 3SA63, and 3SA126; 3SA68, 3SA79, and 3SA123; 3SA58,

3SA86, and 3SA127; 3SA64, 3SA60, and 3SA128; and 3SA75 and 3SA124 evidently belong to the same physiologic races, respectively (Tables 2–5). Isolates are numbered according to a system where an accession number is preceded by 3SA, respectively, indicating *P. r. f. sp. tritici* and South Africa. These isolates could be grouped into six standard races (races 6, 10, 14, 50, 58, and 84) by the scheme of the international register of wheat leaf rust races (7) or into four races (races 3, 6, 9, and 14) according to the unified numeration scheme (4,8). In the present study, international race numbers (4,7) were not allocated to genetically specialized isolates because the *Lr* gene composition of current schemes differs from that of the South African differential set. Thus, isolate numbers were used to refer to different pathotypes of *P. r. f. sp. tritici* in South Africa.

A race (isolate 3SA63) with avirulence/virulence formula *Lr3a,3bg,3ka,11,16,20,24,30/Lr1,2a,15,17* was isolated most frequently (34.9%, Table 4) during 1983, and a similar race (isolates 3SA86 and 3SA127), but with additional virulence for *Lr24*, was isolated most commonly during 1984 (54.1%, Table 5) and 1985 (68.9%, Table 2). A race (isolates 3SA77 and 3SA120) with virulence to *Lr1*, *Lr10*, and *Lr14a* was isolated once from triticale in 1983 and once from Morocco wheat in a trap nursery in 1985.

The surveys indicated differences in the distribution of races. Six races occurred in the Orange Free State, whereas four were identified from the western and southern Cape Province. Drought conditions restricted leaf rust development in the Orange Free State during 1985, but results from the 1984 survey indicated that two races (isolates

**Table 2.** Avirulence/virulence combinations and origin of isolates of *Puccinia recondita* f. sp. *tritici* collected from *Triticum aestivum* and characterized on differential leaf rust resistance (*Lr*) genes in South Africa during 1985

Avirulence/virulence formula	Origin <sup>a</sup> and no. of isolates						%	Type culture number
	WCP and SCP	ECP	OFS	TVL	Natal	Total		
2a,2b,3a,3bg,3ka,11,15,16,17,20,24,30/1,10,14a	0	0	0	0	1	1	0.3	3SA120
3a,3bg,3ka,10,11,14a,16,17,20,24,30/1,2a,2b,15	0	0	0	0	1	1	0.3	3SA121
1,2a,2b,3ka,11,15,17,20,24,30/3a,3bg,10,14a,16	0	6	0	5	4	15	4.8	3SA122
3a,3bg,3ka,10,11,14a,16,17,20,30/1,2a,2b,15,24	0	12	2	0	1	15	4.8	3SA123
3a,3bg,3ka,11,16,20,24,30/1,2a,2b,10,14a,15,17	24	2	4	18	2	50	15.9	3SA126
3a,3bg,3ka,11,16,20,30/1,2a,2b,10,14a,15,17,24	106	59	9	18	25	217	68.9	3SA127
2a,2b,3bg,15,16,17/1,3a,3ka,10,11,14a,20,24,30	1	3	3	9	0	16	5.1	3SA128
Total	131	82	18	50	34	315		

<sup>a</sup>WCP and SCP = western and southern Cape Province, ECP = eastern Cape Province, OFS = Orange Free State, and TVL = Transvaal.

**Table 3.** Avirulence/virulence combinations and origin of isolates of *Puccinia recondita* f. sp. *tritici* collected from *Triticum durum* and characterized on differential leaf rust resistance (*Lr*) genes in South Africa during 1984 and 1985

Avirulence/virulence formula	Origin and no. of isolates			%	Type culture number
	Fish River Valley <sup>a</sup>	Transkei	Total		
1,2a,2b,3ka,11,15,17,20,24,30/3a,3bg,10,14a,16	2	0	2	8.3	3SA122
1,2a,2b,3bg,11,15,16,17,24/3a,3ka,10,14a,20,30	16	0	16	66.7	3SA124
1,2a,3bg,10,11,14a,15,17,24/2b,3a,3ka,16,20,30	2	0	2	8.3	3SA125
3a,3bg,3ka,11,16,20,30/1,2a,2b,10,14a,15,17,24	2	1	3	12.5	3SA127
2a,2b,3bg,15,16,17/1,3a,3ka,10,11,14a,20,24,30	0	1	1	4.2	3SA128
Total	22	2	24		

<sup>a</sup>Durum wheat-producing area in northeastern Cape Province.

**Table 4.** Avirulence/virulence combinations and origin of isolates of *Puccinia recondita* f. sp. *tritici* characterized on differential leaf rust resistance (*Lr*) genes in South Africa during 1983

Avirulence/virulence formula	Origin <sup>a</sup> and no. of isolates						%	Type culture number
	WCP and SCP	ECP	OFS	TVL	Natal	Total (no.)		
2a,3a,3bg,3ka,11,15,16,17,20,24,30/1	0	0	1	0	0	1	2.3	3SA77
1,2a,3ka,11,15,17,20,24,30/3a,3bg,16	3	3	0	0	0	6	14.0	3SA61
3a,3bg,3ka,11,16,17,20,24,30/1,2a,15	0	0	1	0	3	4	9.3	3SA73
3a,3bg,3ka,11,16,20,24,30/1,2a,15,17	10	0	1	3	1	15	34.9	3SA63
3a,3bg,3ka,11,16,17,20,30/1,2a,15,24	0	0	4	0	0	4	9.3	3SA68
3a,3bg,3ka,11,16,20,30/1,2a,15,17,24	1	8	0	0	0	9	20.9	3SA58
2a,3bg,15,16,17/1,3a,3ka,11,20,24,30	0	0	3	1	0	4	9.3	3SA64
Total	14	11	10	4	4	43		

<sup>a</sup>WCP and SCP = western and southern Cape Province, ECP = eastern Cape Province, OFS = Orange Free State, and TVL = Transvaal.

3SA79 and 3SA60) predominated on winter wheat (Table 2). In 1984 and 1985, spring wheat in the Cape Province was also infected by a predominant race (isolates 3SA86 and 3SA127), which constituted 86% and 81% of all isolates collected in that region during those years (Tables 2 and 5).

Eight races were found in the spring and durum wheat production areas of the eastern Cape Province. Pathotype 3SA127 was most prevalent in this region during the survey period. Two races, typified by isolates 3SA124 and 3SA125 (Table 3), were identified only from durum wheat. Pathotype 3SA124 constituted 66.7% of the durum wheat leaf rust isolates. Pathotypes 3SA122, 3SA127, and 3SA128 were also isolated from durum wheat (Table 3). Six races were identified from collections made in the Transvaal and Natal during 1984; the races that occurred in the Transvaal were similar to those found in Natal (Tables 2, 4, and 5).

From surveys of the southern and eastern Cape Province during March 1985, when the annual wheat crop in that region had not yet been sown, 33 isolates from uredinial collections from volunteer plants were established. These isolates yielded three races with virulence

characteristics similar to those of isolates 3SA126, 3SA127, and 3SA128 (Table 2). Two races similar to isolates 3SA123 and 3SA128 were also identified from concurrent collections made from volunteer winter wheat in the eastern Orange Free State. Samples collected during June through August 1985, when several spring wheat fields in the southern Cape Province as well as experimental plots in the Transvaal already were heavily infected with leaf rust, revealed races with avirulence/virulence combinations similar to those of isolates 3SA122, 3SA126, 3SA127, and 3SA128. Survey results obtained during March and August 1985 are combined with results for October to December (Table 2).

The frequency of virulence genes in the population of *P. r. f. sp. tritici* for specific *Lr* genes is presented in Table 6. Virulence for *Lr1*, *Lr2a*, *Lr2b*, *Lr10*, *Lr14a*, *Lr15*, *Lr17*, and *Lr24* was common. Avirulence or virulence to *Lr2a* was always associated with avirulence or virulence to *Lr15*, and similar associations existed among *Lr3ka*, *Lr20*, and *Lr30* in the isolates tested. Virulence to *Lr3bg*, *Lr3ka*, *Lr11*, *Lr16*, *Lr20*, and *Lr30* was rare.

Virulence to seedlings carrying genes

*Lr9*, *Lr19*, *Lr21*, and *Lr26* was not detected in urediniospore composites of field collections. *Lr9* and *Lr19* exhibited infection type 0; whereas *Lr21* and *Lr26* exhibited infection types 2c and 0; to ;1=c, respectively.

## DISCUSSION

Observations on the epidemiology of *P. r. f. sp. tritici* in South Africa confirmed continuous asexual uredinial cycles. Main foci of overwintering inoculum were located in the summer rainfall areas, but precipitation in the Cape Province during the usually dry summer can provide enough volunteer wheat plants for survival of *P. r. f. sp. tritici*. Furthermore, it is unlikely that the aecial stage plays a role in the life cycle of wheat leaf rust in South Africa. In the Cape Province, the production of teliospores, sufficient moisture for their germination, and the growth period of *Anchusa* spp. apparently are not synchronized. However, further research is needed to establish the susceptibility of *A. capensis* and *A. azurea* to infection by teliospores of *P. r. f. sp. tritici*.

Certain epidemiological trends in race distribution and the effect of cultivars on occurrence of races in different agroecological areas were evident. Most

**Table 5.** Avirulence/virulence combinations and origin of isolates of *Puccinia recondita* f. sp. *tritici* collected from *Triticum aestivum* and characterized on different leaf rust resistance (*Lr*) genes in South Africa during 1984

Avirulence/virulence formula	Origin <sup>a</sup> and no. of isolates						Total	%	Type culture number
	WCP and SCP	ECP	OFS	TVL	Natal				
1,2a,3ka,11,15,17,20,24,30/3a,3bg,16	0	1	2	3	3	9	3.7	3SA57	
3a,3bg,3ka,11,16,17,20,24,30/1,2a,15	0	2	6	1	1	10	4.1	3SA78	
3a,3bg,3ka,11,16,20,24,30/1,2a,15,17	8	5	3	11	2	29	11.8	3SA62	
3a,3bg,3ka,11,16,17,20,30/1,2a,15,24	0	2	23	2	6	33	13.4	3SA79	
3a,3bg,3ka,11,16,20,30/1,2a,15,17,24	67	30	13	18	5	133	54.1	3SA86	
2a,3bg,15,16,17/1,3a,3ka,11,20,24,30	3	2	27	0	0	32	13.0	3SA60	
Total	78	42	74	35	17	246			

<sup>a</sup>WCP and SCP = western and southern Cape Province, ECP = eastern Cape Province, OFS = Orange Free State, and TVL = Transvaal.

**Table 6.** Origin and number of isolates of *Puccinia recondita* f. sp. *tritici* virulent to leaf rust resistance genes in South Africa during 1983, 1984, and 1985

Resistance gene	Western and southern Cape Province			Eastern Cape Province			Orange Free State			Transvaal			Natal			Frequency of virulence gene in population (%) <sup>a</sup>		
	1983	1984	1985	1983	1984	1985	1983	1984	1985	1983	1984	1985	1983	1984	1985	1983	1984	1985
<i>Lr1</i>	11	78	131	8	43	78	10	72	18	4	32	45	4	14	30	86.0	93.7	91.5
<i>Lr2a</i>	11	75	130	8	41	74	6	45	15	3	32	36	4	14	29	74.4	81.2	86.1
<i>Lr2b</i>	—	—	130	—	—	76	—	—	15	—	—	36	—	—	29	—	—	86.7
<i>Lr3a</i>	3	3	1	3	10	23	3	29	3	1	3	14	0	3	4	23.3	18.8	13.6
<i>Lr3bg</i>	3	0	0	3	1	8	0	2	0	0	3	5	0	3	4	14.0	3.5	5.2
<i>Lr3ka</i>	0	3	1	0	9	15	3	27	3	1	0	9	0	0	0	9.3	15.3	8.5
<i>Lr10</i>	—	—	131	—	—	9	—	—	16	—	—	50	—	—	32	—	—	72.1
<i>Lr11</i>	0	3	1	0	2	4	3	27	3	1	0	9	0	0	0	9.3	12.5	5.2
<i>Lr14a</i>	—	—	131	—	—	83	—	—	16	—	—	50	—	—	32	—	—	94.5
<i>Lr15</i>	11	75	130	8	41	74	6	45	15	3	32	36	4	14	29	74.4	81.2	86.1
<i>Lr16</i>	3	0	0	3	1	10	0	2	0	0	3	5	0	3	4	14.0	3.5	5.8
<i>Lr17</i>	11	75	130	8	37	62	1	16	13	3	29	36	1	7	27	55.8	64.3	81.2
<i>Lr20</i>	0	3	1	0	9	15	3	27	3	1	0	9	0	0	0	9.3	15.3	8.5
<i>Lr24</i>	1	70	107	8	36	76	7	63	14	1	20	27	0	11	26	39.5	78.4	75.8
<i>Lr30</i>	0	3	1	0	9	15	3	27	3	1	0	9	0	0	0	9.3	15.3	8.5
No. of isolates tested	14	78	131	11	51	97	10	74	18	4	35	50	4	17	34			

<sup>a</sup>Genes *Lr2b*, *Lr10*, and *Lr14a* were not tested during 1983 and 1984.

races of *P. r. f. sp. tritici* occurred throughout the country. However, the races typified by isolates 3SA120, 3SA124, and 3SA125 were not widespread; the last two apparently were adapted to durum wheat. Differential fitness and selection among races identified in our study were emphasized by the frequent isolation of one race during consecutive surveys of the Cape Province in 1985. The common occurrence of this race, which was virulent to *Lr1*, *Lr2a*, *Lr2b*, *Lr10*, *Lr14a*, *Lr15*, *Lr17*, and *Lr24*, could partly be ascribed to the extreme susceptibility of all spring wheat cultivars recommended in South Africa. However, this race is avirulent to the local winter wheat cultivars Betta, SST102, and Karee, which accordingly acted as selective hosts for a different race (similar to isolate 3SA128) in the Orange Free State. Similarly, the spring wheat cultivar Zaragoza was selective for another race (isolate 3SA122) found mostly in irrigated areas in the Transkei, Natal, and Transvaal. The genes for resistance to leaf rust in the current spring and winter wheat cultivars are not known.

Comparison of present races with those described by Verwoerd (15) or with pathogenicity patterns in the United States (8) and Canada (12) is not possible because different differential hosts were used in these studies. However, if we do not consider Brevit, Loros, and Mediterranean because these were not included as differential hosts in our study, race 15 identified in 1937 (15) corresponds with isolates 3SA122 and 3SA124 and race 91 corresponds with isolate 3SA128. Harder (6) identified five races in Kenya, but the lack of avirulence in the East African isolates for *Lr10* or *Lr17* and the lack of virulence for the gene in Aniversario (*Lr3ka*) distinguished those races from the current population of *P. r. f. sp. tritici* in South Africa.

If pathogenicity of isolates to individual *Lr* genes is considered, certain similarities and differences between the South African and North American (8,12) leaf rust populations are evident. In both populations, virulence to *Lr1*, *Lr2a*, *Lr10*, and *Lr14a* commonly occurs, whereas virulence to *Lr3ka*, *Lr11*, *Lr16*, and *Lr30* is rare. *Lr19* appears universally resistant. *Lr21* is effective in South Africa and Canada but not in the United States. *Lr26* confers resistance to all isolates tested in South Africa and the United States, but virulence to this gene was detected in Canada in 1984. The lack of virulence in South African isolates for *Lr9* also distinguishes the local population of *P. r. f. sp. tritici* from North American races. Furthermore, a large percentage of North American isolates are virulent to *Lr3a*, whereas in South Africa, the opposite was found. Conversely, in the United States and Canada, virulence to *Lr17* and *Lr24* seldomly occurs but is common in South Africa.

Among the *Lr* genes evaluated in our study, *Lr9*, *Lr19*, *Lr21*, and *Lr26* would be most useful as single-gene resistance sources in South Africa. Ideally, paired combinations of these genes should be incorporated into new cultivars. However, effective use of resistance sources also depends on the absence of linkage between such genes and undesirable agronomic and quality characteristics. In view of the restricted number of effective seedling genes, other sources of genetic resistance to leaf rust should be considered. Adult-plant resistance is frequently overlooked in seedling evaluations, and more detailed investigations could identify effective and durable types of resistance.

Genetic resistance to leaf rust should be a primary objective of South African wheat-breeding programs. Although the disease could be controlled with fungicides, the mean yield of cultivars in high-

risk leaf rust areas usually is too low to justify the cost of chemical control.

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